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SEDAR51-RD-03

June 2016

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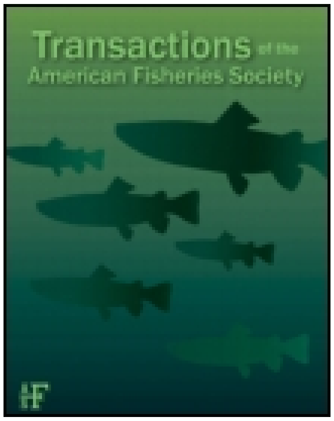

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Transactions of the American Fisheries Society
Publication details, including instructions for authors and subscription information:
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Published online: 30 Jul 2015.

To cite this article: Kerry E. Flaherty-Walia, Theodore S. Switzer, Brent L. Winner, Amanda J. Tyler-Jedlund & Sean F. Keenan (2015) Improved Ability to Characterize Recruitment of Gray Snapper in Three Florida Estuaries along the Gulf of Mexico through Targeted Sampling of Polyhaline Seagrass Beds, Transactions of the American Fisheries Society, 144:5, 911-926, DOI: 10.1080/00028487.2015.1054516

To link to this article: http://dx.doi.org/10.1080/00028487.2015.1054516

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Transactions of the American Fisheries Society 144:911–926, 2015
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ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2015.1054516

ARTICLE

Improved Ability to Characterize Recruitment of Gray Snapper in Three Florida Estuaries along the Gulf of Mexico through Targeted Sampling of Polyhaline Seagrass Beds

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Abstract

Estuarine-dependent Gray Snapper *Lutjanus griseus* support extensive recreational fisheries in estuarine and coastal waters throughout the eastern Gulf of Mexico. Multiyear fisheries-independent monitoring data collected in three Florida estuaries can be used to estimate the strength of juvenile Gray Snapper recruitment, which has been critical to assessments of other fish populations. Earlier evaluation of these data indicated that Gray Snapper inhabit polyhaline seagrass beds, which are underrepresented in ongoing monitoring efforts. During this study, in addition to the routine monitoring of shorelines and channel habitats, sampling of shoal and deepwater polyhaline seagrass habitats was implemented using 183-m haul seines and 6.1-m otter trawls. The incorporation of polyhaline seagrass surveys from 2008 through 2011 allowed a more thorough sampling of the Gray Snapper population, resulting in improved catch rates, increased frequency of occurrence, and a substantial reduction of the coefficient of variation for CPUE in most years and estuarine systems. Habitat-based sampling of polyhaline seagrass habitats also provided additional data for annual abundance indices and therefore improved the ability to characterize the strength of recruitment for Gray Snapper over time. These results demonstrated that periodically reevaluating habitat-based stratification approaches to estimate fish abundance indices from long-term surveys can lead to more precise estimates and greater numbers of measured individuals, which are key components of successful monitoring programs.

Reef fishes support important recreational and commercial fisheries on the Gulf of Mexico and Atlantic coasts. Recent studies have indicated that many exploited reef fishes along the southeastern coast of the United States are being overfished (Ault et al. 1998, 2005a, 2006). For Gray Snapper *Lutjanus griseus* in southeastern U.S. waters, the bulk of landings are made in Florida, especially in the southern portion of the state, where they support an increasingly important recreational fishery (Ault et al. 2005b). Gray Snapper reach maturity at 175–198 mm SL between 2 and 3 years of age (Starck and Schroeder 1971; Manooch and Matheson 1981; Domeier et al. 1996). The species is currently managed with a recreational minimum size limit of 254 mm (10 in) TL in Florida waters and 305 mm (12 in) TL in federal waters, and a bag limit of five fish per person as part of the daily aggregate snapper bag limit of 10 fish. On the West Florida shelf, the most common Gray Snapper ages reported for the recreational fishery were 5–12 years with a maximum of 26 years (Allman and Goetz 2009). Despite heavy fishing pressure, Gray Snapper stocks appear stable, based partly on the evaluation of fisheries-independent indices of juvenile abundance and a consideration of their size at maturity (FWC FWRI 2010). Variability in young of the year (age 0) Gray Snapper abundance may be attributed to fluctuations in factors such as fecundity, larval mortality, larval transport, habitat availability, and survival rates in the estuary (Warlen et al. 1998; Epifanio and Garvine 2001). Fisheries-independent indices of juvenile abundance have proven invaluable in the assessment of other important fisheries in Florida, e.g., Common Snook *Centropomus undecimalis* (Muller and Taylor 2013), Red Drum *Sciaenops ocellatus*

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Received October 24, 2014; accepted May 14, 2015

(Murphy and Munyandorero 2009), and Yellowtail Snapper *Ocyurus chrysurus* (Muller et al. 2003), and may hold promise for forecasting fisheries recovery (Winner et al. 2014).

Recreationally and commercially important groupers and snappers, including Gray Snapper, use seagrass beds as nursery habitat (Arrivillaga and Baltz 1999; Nagelkerken et al. 2001; Ault et al. 2006; Acosta et al. 2007; Casey et al. 2007). Gray Snapper spawn during the summer (May–September) in offshore waters around structured reef habitats, and larvae settle out of their planktonic stage into structurally complex estuarine habitats such as seagrass beds (Allman and Grimes 2002; Tzeng et al. 2003; Denit and Sponaugle 2004a), where they remain as juveniles (Nagelkerken et al. 2000; Cocheret de la Morinière et al. 2002; Whaley et al. 2007; Faunce and Serafy 2008). Subadults transition to mangrove and channel habitats before migrating to offshore reefs (Starck and Schroeder 1971). Studies in gulf estuarine systems have indicated that juvenile and subadult Gray Snapper use areas that have a high percentage of cover by seagrass and other submerged aquatic vegetation (SAV) (Chester and Thayer 1990; Flaherty et al. 2014). Increased seagrass cover in an area suggests that protection of fish from predators is greater there than in other habitats (Orth et al. 1984). However, seagrass leaf density varies seasonally, so characteristics in addition to seagrass cover may also be important in determining juvenile fish abundance. For some fishes, seagrass bed architecture, seagrass species composition, and water quality can influence the value of seagrass as habitat (Bell et al. 1987, 1988; Robbins and Bell 1994; Raposa and Oviatt 2000; Jelbart et al. 2007). For others, including Gray Snapper, juvenile abundance may be more strongly correlated with the geographic location of the seagrass bed relative to sources of larvae and the salinity regime than with bed architecture (Bell et al. 1988; Flaherty et al. 2014). By examining habitat types known to contain Gray Snapper, we can better assess which microhabitat characteristics are most important in distinguishing patterns of habitat use for this species (Baltz 1990).

Retrospective analyses of long-term (1996–2009), fisheries-independent seine data collected in Florida Gulf Coast estuaries have indicated that Gray Snapper were most commonly collected in warm waters (primarily a function of the months of peak estuarine occupancy) with high salinity and high coverage of SAV (Flaherty et al. 2014). Other recent (2008–2010) seine surveys have shown that Gray Snapper were more likely to characterize seagrass shoal fish communities than mangrove shoreline fish communities (DeAngelo et al. 2014). Polyhaline seagrass shoals with relatively steep slopes and deep (>1 m) seagrass beds have traditionally been underrepresented in monitoring efforts relative to their proportional area due to established methodology and the difficulty of sampling in deeper water (DeAngelo et al. 2014; Flaherty et al. 2014). Although the slopes and depth of seagrass beds in Florida are moderate and shallower than seagrass beds examined in other studies (Francour 1997; Smith et al. 2012), this difference is biologically meaningful in shallow, relatively eutrophic estuaries such as those found on the Gulf Coast. Possibly due to the undersampling of these polyhaline seagrass beds, maxima in annual relative abundance of juveniles were not well correlated with those for subadults in some estuaries (Flaherty et al. 2014). This disconnect, in turn, limits the value of using indices of juvenile abundance to forecast abundance in the offshore fishery. Determining the estuarine occupancy of larger subadults and adults that are associated with these habitats will improve indices of abundance and our understanding of Gray Snapper habitat use. In addition, the Magnuson–Stevens Fishery Conservation and Management Act dictates that essential fish habitat be identified and described for fishery management plans, and this study investigates the importance of an additional undersampled seagrass habitat that may be worthy of protection.

Accordingly, the objectives of this study were to implement habitat-based monitoring that targeted polyhaline seagrass habitats and to characterize temporal and spatial variability in Gray Snapper recruitment and habitat use for three estuarine systems on the Florida Gulf Coast. This study was also designed to determine whether incorporating these polyhaline seagrass areas into a monitoring design would reduce variability of annual indices of abundance for Gray Snapper.

METHODS

Study sites.—We investigated patterns of habitat use by Gray Snapper in three estuarine systems on the Gulf of Mexico coast of Florida (Apalachicola Bay, Tampa Bay, and Charlotte Harbor; Figure 1). These estuaries are proximate to the West Florida Shelf, a broad expanse of ocean bottom containing much of the natural hard-bottom habitat used by reef fishes in the Gulf of Mexico (Briggs 1958; McEachran and Fechhelm 1998). They are also shallow, bounded by barrier islands, and contain seagrass meadows consisting of shoal grass *Halodule wrightii*, turtle grass *Thalassia testudinum*, and manatee grass *Syringodium filiforme*. Shoreline vegetation in Apalachicola Bay consists largely of salt-marsh habitat (primarily cordgrass *Spartina* spp. and black needlerush *Juncus roemerianus*), while shoreline vegetation for the two more southern estuarine systems consists largely of fringing mangroves (predominantly red mangrove *Rhizophora mangle* and black mangrove *Avicennia germinans*). For further details on the respective study areas, see Switzer et al. (2012).

Field methods.—The state of Florida conducts long-term monthly fisheries-independent monitoring (FIM) spatially stratified within each bay and restricted by depth using several gear types, including a 183-m haul seine and a 6.1-m otter trawl (Purtlebaugh and Rogers 2007; Winner et al. 2010; Flaherty et al. 2014). A 183 × 2.5-m, center-bag haul seine (38-mm stretched mesh) is used to sample large-bodied fish (>100 mm SL) along shoreline habitats in waters <2.5 m deep. The net is set in a rectangular shape by using a boat

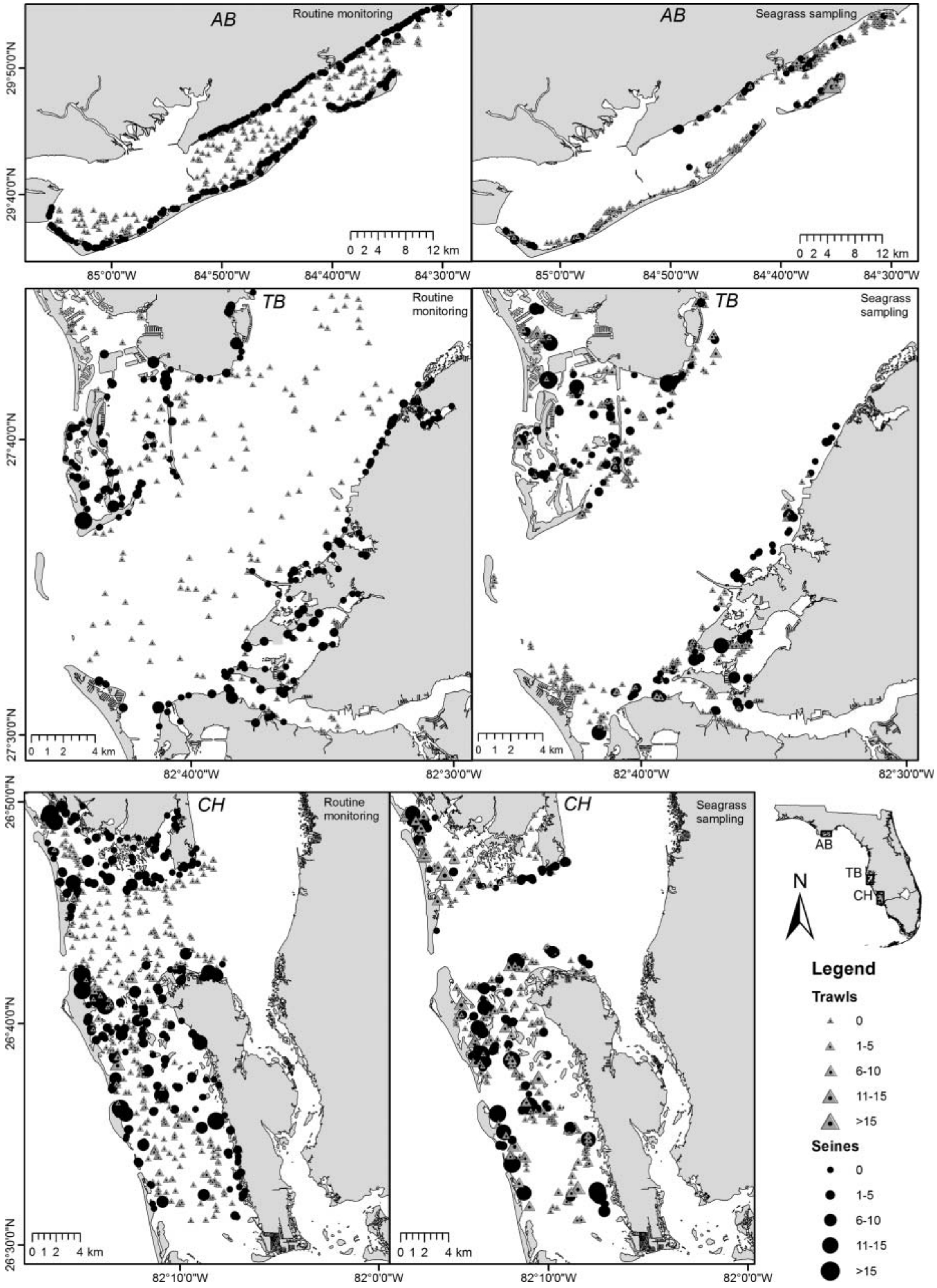

FIGURE 1. The location of the three estuarine systems on the Florida Gulf Coast (AB: Apalachicola Bay; TB: Tampa Bay; CH: Charlotte Harbor) in which monthly stratified-random sampling of Gray Snapper was conducted. The number of Gray Snapper collected in each estuary using trawls (gray triangles) and seines (black circles) during routine monitoring (left panels) and seagrass sampling (right panels) from May through November 2008–2011 are shown. *x*- and *y*-axes are longitude and latitude, respectively.

along shoreline habitats (i.e., mangroves, marsh grass, seawalls: Winner et al. 2010), and the dimensions of the area sampled by the net (approximately 40 × 103 m, or 4,120 m^2) are standardized by marking 40 m from each end of the net to designate the corner locations. The 6.1-m otter trawl (38-mm stretched mesh) is used to sample demersal habitats in waters 1.8–7.6 m deep and is towed for 10 min and approximately 0.2 nautical miles (370 m), sampling an area of approximately 1,482 m^2. Actual distance towed was measured by differential GPS, and measurement ended as soon as net retrieval began. Smaller-bodied fish (<100 mm SL) are typically collected with the 6.1-m otter trawl, which has a 3-mm mesh liner in the cod end; nevertheless, larger fish are sometimes collected with this type of gear. These surveys are not explicitly designed to target the estuarine-dependent juvenile life history phase of reef fish and have not been stratified based on the presence of seagrass habitat. This long-term monitoring program is subsequently referred to as *routine monitoring.* Historically, few reef fish have been collected using the 6.1-m otter trawl, although Gray Snapper were present in approximately 12% of the 183-m haul-seine samples collected from 1996 through 2009 (Flaherty et al. 2014).

Results from studies in the eastern Gulf of Mexico (Koenig and Coleman 1998; Fitzhugh et al. 2005; Casey et al. 2007) were used to design a complementary FIM survey to enhance our ability to characterize populations of juvenile Gag *Mycteroperca microlepis* and other estuarine-dependent, seagrass-associated fishes, including Gray Snapper. Available bathymetry and SAV-coverage (Yarbro 2013) data were used to define a sampling universe of 0.2 × 0.2-km sampling units that contained seagrass habitats from which monthly sampling sites were randomly selected (ArcGIS: Hawth's tools random selection method). The universe data selected by ArcGIS was updated periodically as new seagrass mapping data became available, and appropriate conditions were verified at the time of sampling. The present study, conducted during 2008–2011 in conjunction with routine monitoring, incorporated both the 183-m haul seine (DeAngelo et al. 2014) and the 6.1-m otter trawl (subsequently called seines and trawls, respectively) to target polyhaline seagrass habitats (i.e., generally salinities >18 psu; SAV covering more than 50% of the bottom sampled) that had been underrepresented in routine FIM surveys before 2008. This complementary survey targeting polyhaline seagrass beds is subsequently referred to as *seagrass sampling.* Unlike routine monitoring in which the seine was set and pursed together along a shoreline, the seine was set parallel to seagrass shoals (≤0.5 m deep, often exposed) not associated with a shoreline during seagrass sampling. Seines were set on shoals where the difference (slope) between the wing depth (depth at which the ends of the seine were joined together along the shoal, the shallowest portion of the net deployment) and the bag depth (the deepest portion of the net) was at least 0.5 m (DeAngelo et al. 2014). The trawl was used to sample deep seagrass habitats in waters between 1.0 and 7.6 m deep and was towed for 5 min and approximately 0.1 nautical mile (185 m), sampling an area of approximately 741 m^2. In waters less than 1.8 m deep, the trawl was towed in an arc to prevent disturbance of the sampled substrate by propeller wash. Actual distance towed was measured by differential GPS, and measurement ended as soon as net retrieval began. All monthly sampling in these seagrass habitats was conducted from May through November, the period of peak estuarine occupancy by juvenile reef fishes, including Gray Snapper (Switzer et al. 2012; Flaherty et al. 2014).

Gray Snapper collected in each sample were counted, and up to 40 randomly selected individuals per sample were measured to the nearest millimeter SL. Location, water depth, and water quality were recorded at each sampling site; for seines, measurements were taken at the bag (bag depth); whereas for trawls, measurements were taken at the point where the trawl was first put in the water (starting depth). Temperature (°C), salinity (psu), and dissolved oxygen (mg/L) were recorded at the surface and bottom and at 1.0-m depth intervals using a water quality data sonde and averaged over those depth intervals for each sample. For seine samples, wing depth and slope were also recorded. Date, time, and habitat variables (bottom type and percentage SAV cover) were recorded for each net set at the time of sampling (DeAngelo et al. 2014). Bottom type (sand, mud, shell, or mixed) and SAV cover for both gears were determined qualitatively by visual (sight or underwater camera) or tactile (by hand or anchor) methods at four or more points within the sampling area.

*Analytical methods.—*To facilitate comparability, a subset of routine monitoring data were used that included only data collected from the same temporal and spatial extent as the seagrass sampling implemented from May through November in 2008–2011. The relative effectiveness of the routine monitoring and the seagrass sampling while collecting Gray Snapper was compared. This comparison looked at a summary of environmental conditions, overall sampling effort, number of individuals collected, frequency of occurrence, CPUE (individuals per 100 m^2), and size structure. Overall CPUE and length-frequency distributions of Gray Snapper for each type of gear and each estuarine system were compared between sampling types (routine monitoring versus seagrass sampling) using the nonparametric Kruskal–Wallis test and Kolmogorov–Smirnov (K–S) test, respectively ($\alpha = 0.05$) with the program PROC NPAR1WAY (SAS Institute 2006).

Based on monthly length-frequency distributions, gear type, and gear selectivity, three data sets were constructed: small-bodied Gray Snapper (≤100 mm SL, referred to as *juveniles*) collected with (1) trawls during the recruitment window of August–November, and large-bodied Gray Snapper (101–250 mm SL, referred to as *subadults* but acknowledging that some of the larger fish may have reached maturity) collected with (2) trawls or (3) seines in all months (May–November). For each data set, annual nominal CPUE and coefficients of variation (CV = 100 · SD/mean) were calculated by sampling type for each estuarine system. Due to differences in the areas sampled, nominal CPUE was calculated for trawl samples as the number of individuals per 100 m^2 of area sampled. The CPUE for seine samples was calculated as the number of individuals per haul. Differences in CV between sampling types were calculated by year for all estuarine systems.

For all three data sets, annual indices of abundance (IOA) of Gray Snapper combined over sampling types were constructed for Apalachicola Bay (juvenile Gray Snapper only, due to small numbers of subadults collected), Tampa Bay, and Charlotte Harbor using generalized linear modeling analyses. Indices were calculated as the number of individuals per haul for both gears, with the area sampled (effort) as a covariate for trawls. The relative abundance of Gray Snapper represents count data, the distribution of which is bound by zero and therefore often highly nonnormal. Accordingly, generalized linear models based on the Poisson distribution and the negative binomial distribution were fit to the data, and residual diagnostics and goodness-of-fit statistics were examined to determine the most appropriate model. For all three estuaries, the model based on the negative binomial distribution was the most appropriate. For seine data, the year, sampling type (routine monitoring versus seagrass sampling), and bottom type were used in the model as categorical explanatory variables, and temperature, salinity, dissolved oxygen, bag depth, wing depth, and SAV cover were used as covariates. For trawl data, year, sampling type, and bottom type were used in the model as categorical explanatory variables, and temperature, salinity, dissolved oxygen, starting depth, and effort (area of bottom sampled) were used as covariates. Interactions between sampling type and variables associated with sampling type (bag or starting depth, effort, SAV cover, and wing depth) were also tested for significance. With the exception of year and variables associated with significant interactions, variables that were not significant ($\alpha = 0.05$) and did not improve model fit based on the Akaike's information criterion (AIC) value were removed, and the analysis was repeated until the most parsimonious model remained. For each estuarine system, annual least-square mean estimates (±SE) of relative abundance were calculated and plotted to assess temporal variability in recruitment for 2008–2011. All analyses were fit using the GLIMMIX procedure and SAS software (SAS Institute 2006).

RESULTS

Most environmental variables (temperature, salinity, and dissolved oxygen) were similar between routine monitoring and seagrass sampling sites, but the sites clearly differed in water depth and SAV cover, mostly due to differences in methodology by sampling type (Table 1).

TABLE 1. Mean ± SE physicochemical conditions and habitat metrics observed during routine monitoring and seagrass sampling using seines and trawls in three Gulf of Mexico estuaries (AB: Apalachicola Bay; TB: Tampa Bay; CH: Charlotte Harbor). Slope and wing depth are measured only during seine sampling, and depth equates to bag depth for seines and starting depth for trawls.

		Seines		Trawls	
Environmental variable	Bay	Routine	Seagrass	Routine	Seagrass
Temperature (°C)	AB	26.95 ± 0.24	26.49 ± 0.41	26.66 ± 0.27	26.70 ± 0.27
	TB	27.99 ± 0.24	27.76 ± 0.26	27.78 ± 0.25	27.70 ± 0.20
	CH	28.39 ± 0.20	28.09 ± 0.26	28.18 ± 0.17	28.40 ± 0.22
Salinity (psu)	AB	28.64 ± 0.26	29.79 ± 0.39	29.48 ± 0.24	29.50 ± 0.26
	TB	31.47 ± 0.22	32.30 ± 0.19	32.04 ± 0.20	32.60 ± 0.16
	CH	33.36 ± 0.25	33.36 ± 0.32	33.84 ± 0.19	34.00 ± 0.22
Dissolved oxygen (mg/L)	AB	7.24 ± 0.11	7.27 ± 0.14	6.74 ± 0.09	7.20 ± 0.09
	TB	6.63 ± 0.16	6.67 ± 0.10	6.56 ± 0.10	6.80 ± 0.09
	CH	6.92 ± 0.13	7.34 ± 0.14	6.48 ± 0.05	7.00 ± 0.11
Depth (m)	AB	0.95 ± 0.02	1.37 ± 0.05	3.47 ± 0.08	1.60 ± 0.03
	TB	1.02 ± 0.03	1.46 ± 0.03	3.75 ± 0.11	1.70 ± 0.04
	CH	1.13 ± 0.03	1.41 ± 0.04	2.87 ± 0.05	1.60 ± 0.03
SAV cover (%)	AB	40.75 ± 1.95	72.14 ± 1.69	1.48 ± 0.72	70.70 ± 1.45
	TB	69.27 ± 2.25	82.76 ± 1.10	14.44 ± 7.24	76.90 ± 1.06
	CH	71.60 ± 1.85	83.72 ± 1.34	2.91 ± 1.22	90.20 ± 1.12
Wing depth (m)	AB	0.22 ± 0.01	0.61 ± 0.02		
	TB	0.32 ± 0.02	0.59 ± 0.02		
	CH	0.50 ± 0.02	0.47 ± 0.02		
Slope (m)	AB	0.73 ± 0.03	0.75 ± 0.05		
	TB	0.69 ± 0.03	0.86 ± 0.03		
	CH	0.63 ± 0.03	0.93 ± 0.04		

TABLE 2. Summary (2008–2011) of seasonal (monthly from May through November) sampling effort and overall catch data by seine or trawl for Gray Snapper from the polyhaline region of three estuarine systems along the Florida Gulf coast.

	Routine monitoring			Seagrass sampling		
Estuarine system	Total samples	Samples containing Gray Snapper (% frequency)	Gray Snapper collected	Total samples	Samples containing Gray Snapper (% frequency)	Gray Snapper collected
			Seine			
Apalachicola Bay	314	13 (4.1%)	21	112	3 (2.7%)	4
Tampa Bay	242	67 (27.7%)	181	196	76 (38.8%)	341
Charlotte Harbor	258	123 (47.7%)	747	171	93 (54.4%)	587
Totals	814	203 (24.9%)	949	479	172 (35.9%)	932
			Trawl			
Apalachicola Bay	215	1 (0.5%)	1	224	19 (8.5%)	48
Tampa Bay	174	7 (4.0%)	14	280	69 (24.6%)	191
Charlotte Harbor	339	35 (10.3%)	69	229	119 (52.0%)	500
Totals	728	43 (5.9%)	84	733	207 (28.2%)	739

The gear types used in this study were effective at capturing Gray Snapper. A total of 814 seine samples were collected along shoreline habitats (routine monitoring) and 479 were collected over seagrass shoal habitats (seagrass sampling); of these samples, 24.9% and 35.9%, respectively, contained Gray Snapper (Table 2; Figure 1). A total of 728 trawl samples were collected from predominantly unvegetated habitats (routine monitoring) and 733 were collected over seagrass habitats (seagrass sampling); of these samples, 5.9% and 28.2%, respectively, contained Gray Snapper (Table 2; Figure 1). Overall, Gray Snapper were most frequently collected in Charlotte Harbor, followed by Tampa Bay. Numbers collected in Apalachicola Bay were minimal, reinforcing previously documented latitudinal trends in Gray Snapper abundance (Allman and Goetz 2009; Flaherty et al. 2014).

Nominal overall CPUE of Gray Snapper was significantly higher at seagrass sampling sites than at routine monitoring sites for all estuarine systems and gear types (PROC NPAR1-WAY; K–W tests: $\chi^2 = 8.64$–141.1, df = 1, $P < 0.05$), except for seine data from Apalachicola Bay and Charlotte Harbor, where CPUE was similar for both sampling types (Figure 2). Increases in CPUE were most pronounced for trawl surveys conducted during seagrass sampling. Length-frequency summaries indicated that subadult Gray Snapper (101–250 mm SL) were common in seine and trawl sampling (Figure 3) in Tampa Bay and Charlotte Harbor but rare in Apalachicola Bay. The majority of juvenile Gray Snapper ($\leq$100 mm SL), however, were collected by trawl sampling (Figure 3) and exhibited peak recruitment from August through November (Figure 4). Overall and estuarine-specific size structure was significantly different between sampling types (K–S distribution tests: $P < 0.05$ for both gear types) among most combinations of estuary and gear type (Figure 3; note that Apalachicola Bay size structures were not compared due to small sample size).

For Tampa Bay and Charlotte Harbor, annual indices of abundance (combined IOA) determined from generalized linear modeling analyses incorporating both sampling types indicated that year, sampling type, bag depth, temperature, and dissolved oxygen significantly influenced the number of subadult Gray Snapper collected in seine samples and that salinity

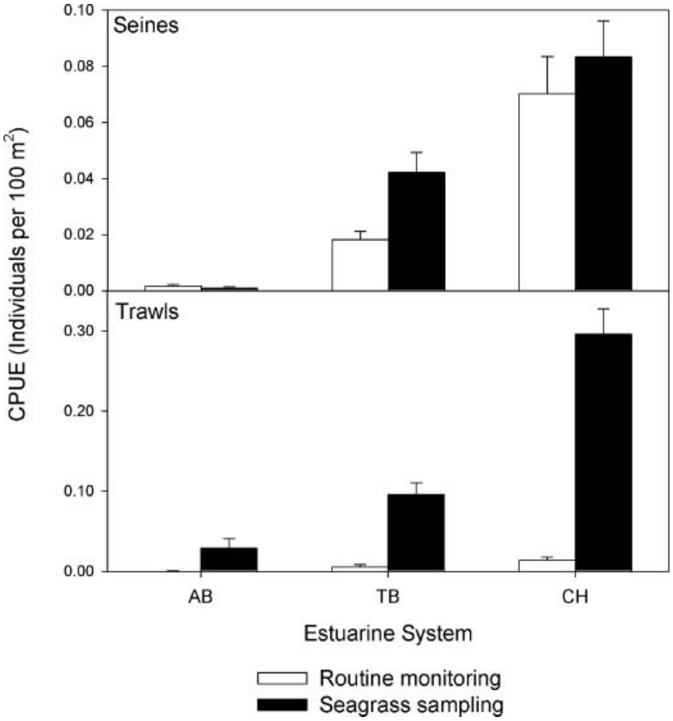

FIGURE 2. Summary of mean + SE CPUE (number of individuals per 100 m^2) of Gray Snapper from routine monitoring and seagrass sampling using seines and trawls from 2008 through 2011, by estuarine system (AB: Apalachicola Bay; TB: Tampa Bay; CH: Charlotte Harbor). Note differences in *y*-axis scale.

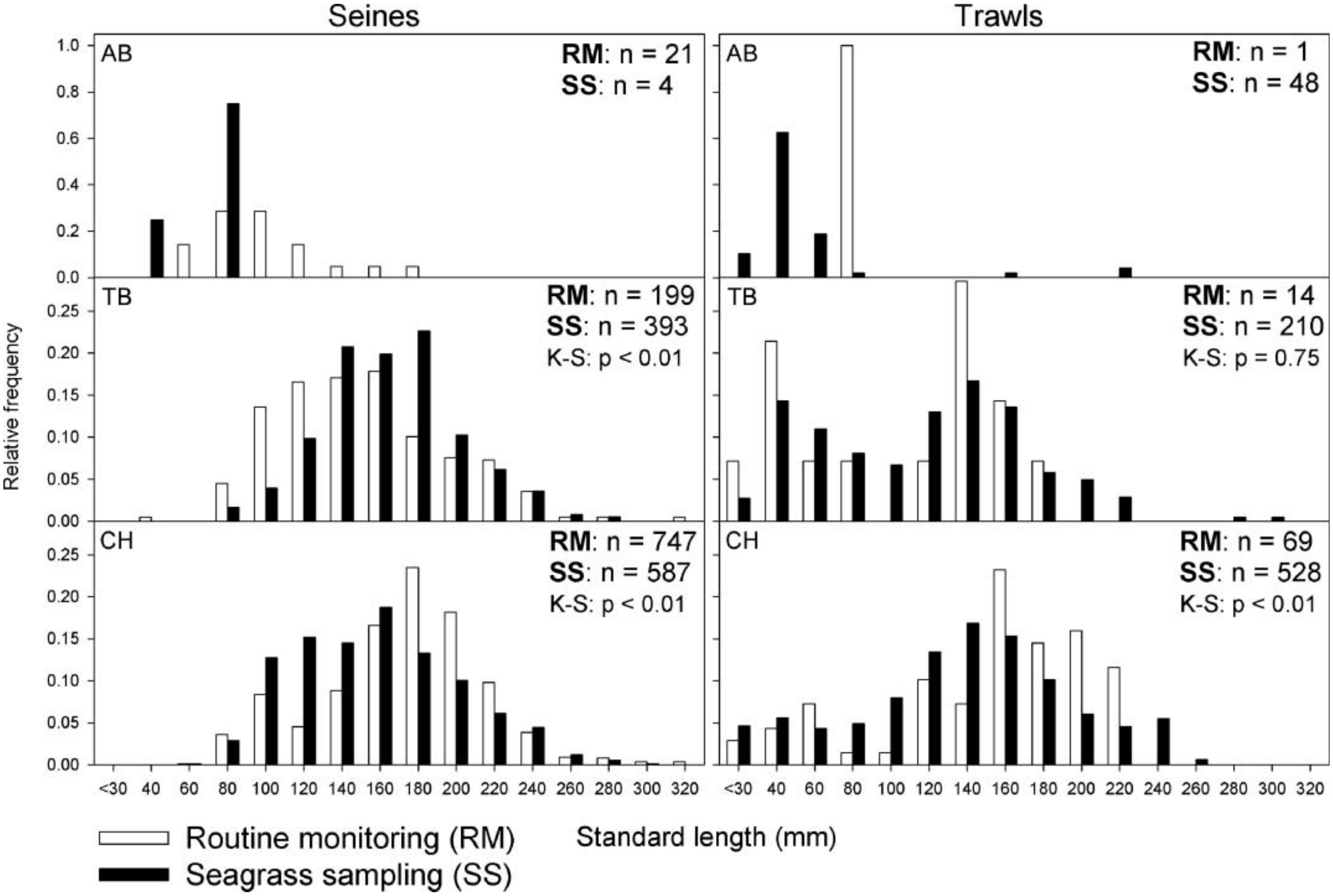

FIGURE 3. Length-frequency distributions of Gray Snapper collected during routine monitoring (RM) and seagrass sampling (SS) using seines (left panels) and trawls (right panels) from 2008 to 2011 by estuarine system (AB: Apalachicola Bay, TB: Tampa Bay, CH: Charlotte Harbor). Number of individuals captured during each sampling type and *P*-values for estuarine-specific K–S tests comparing length-frequency distributions are indicated in the upper right corner of each panel (note that K–S comparisons for Apalachicola Bay were not conducted due to small sample sizes).

did not (Table 3). In Charlotte Harbor, bottom type as well as interactions between sampling type and SAV cover and between sampling type and wing depth were significant, while in Tampa Bay, wing depth was significant. Although Gray Snapper were typically more abundant over seagrass shoals, the combined IOA for Charlotte Harbor (Figure 5) and separate nominal CPUEs for both sampling types exhibited similar trends (i.e., high abundance in 2008 followed by lower abundance in 2010). The incorporation of seagrass sampling in Tampa Bay (i.e., combined IOA), however, revealed a slightly different pattern of abundance (i.e., most abundant in 2008 and least abundant in 2010) than was evident by examining CPUE separately for the two sampling types (Figure 5). Although some of the patterns in annual CPUE between sampling types were consistent, seagrass sampling using seines resulted in reductions in the CV in Gray Snapper CPUE in at least one estuary in all years except 2010 (Figure 6).

Routine monitoring of mostly unvegetated channel habitats and seagrass sampling using a trawl revealed that juvenile and subadult Gray Snapper CPUEs were markedly higher over deepwater polyhaline seagrass beds in most years. However, it was difficult to discern annual patterns in abundance from routine monitoring data since no or few Gray Snapper were collected in certain years (Figures 7, 8). Generalized linear modeling analyses incorporating both sampling types provided a more robust representation of annual abundance trends, with year and starting depth retained in models of juvenile and subadult Gray Snapper abundance in trawl samples over all estuarine systems (Tables 4, 5). For juveniles, sampling type, effort, bottom type, and the interaction between sampling type and starting depth also influenced abundance in some estuaries (Table 4). For subadults, temperature significantly influenced abundance in both estuaries, and the interaction between sampling type and starting depth was important in Charlotte Harbor, while dissolved oxygen was important in Tampa Bay (Table 5). The incorporation of seagrass sampling from 2008 through 2011 made possible the

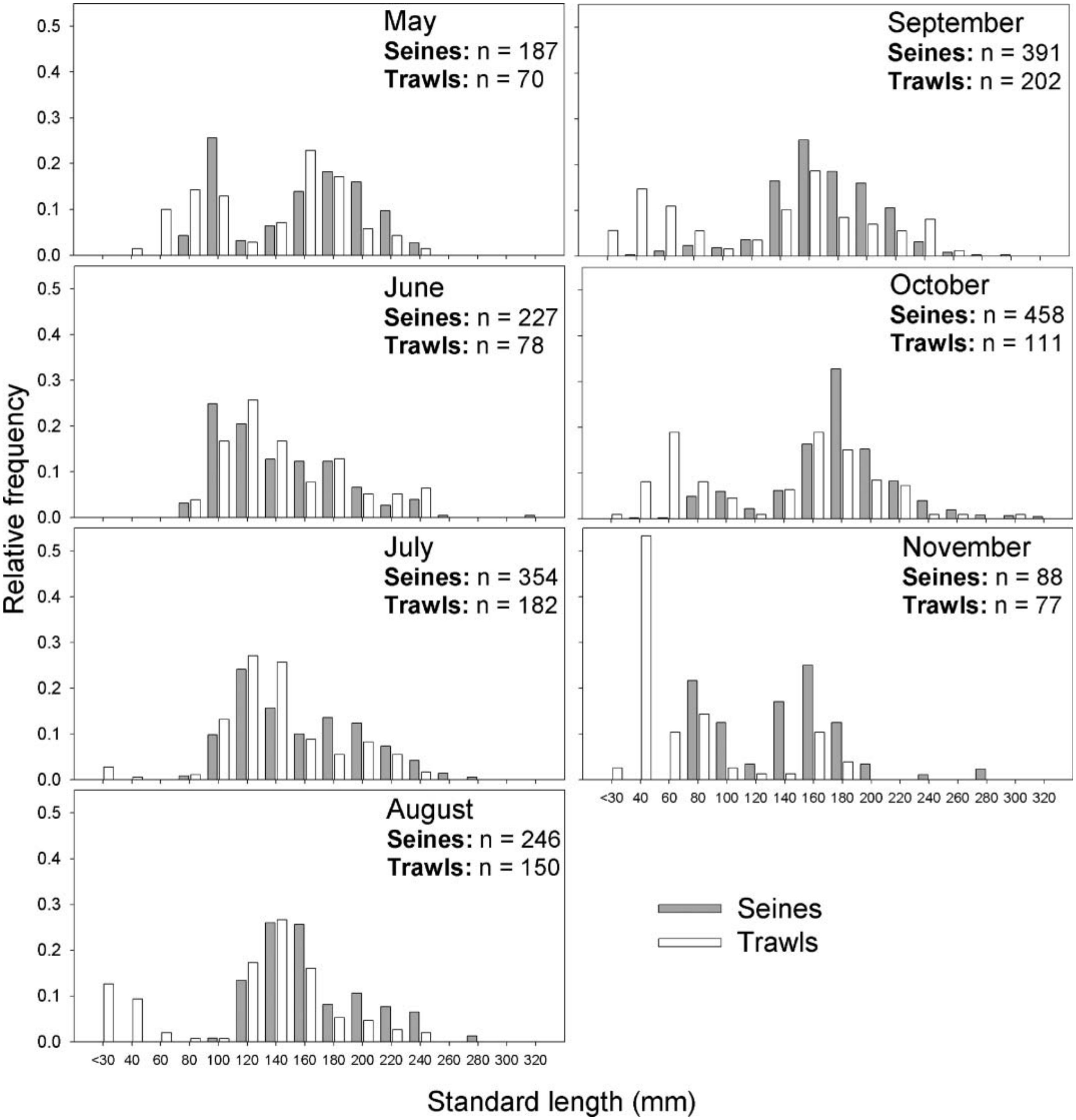

FIGURE 4. Monthly length-frequency distributions, by gear type, of Gray Snapper collected during both routine monitoring and seagrass sampling from 2008 through 2011 for the three estaurine systems combined. Number of individuals captured with each gear type are indicated in the upper right corner of each panel.

calculation of indices of abundance using trawl data, and in most cases these annual indices of abundance mirrored the CPUE from seagrass sampling (Figures 7, 8). A strong year-class of juvenile Gray Snapper was evident in 2011 in Apalachicola Bay and in 2009 for Tampa Bay and Charlotte Harbor (Figure 7). The same trends in subadult Gray Snapper annual abundance from combined IOAs documented above from seine samples were reflected in trawl samples (Figure 8). Predictably, for most years and estuarine systems examined, seagrass sampling with trawls

TABLE 3. Results of generalized linear modeling analyses indicating the effects of year and several habitat and physicochemical variables on CPUE (number of individuals per seine) of subadult Gray Snapper in two estuarine systems in the eastern Gulf of Mexico including data collected during seagrass sampling from May through November 2008–2011; ndf = numerator degrees of freedom, ddf = denominator degrees of freedom, NS = not significant.

		Tampa Bay (ddf = 422)		Charlotte Harbor (ddf = 400)	
Model variable	ndf	*F*	*P*	*F*	*P*
Year	3	5.07	0.0018	5.77	0.0007
Sampling type	1	15.45	<0.0001	14.81	0.0001
Sampling type × SAV cover	1	NS	NS	7.47	0.0065
Sampling type × Wing depth	1	NS	NS	5.32	0.0216
Bottom type	3	NS	NS	3.23	0.0225
Bag depth (m)	1	25.23	<0.0001	26.4	<0.0001
Wing depth (m)	1	8.34	0.0041	3.24	0.0728
SAV cover (%)	1	NS	NS	0.04	0.8437
Temperature (°C)	1	20.35	<0.0001	23.75	<0.0001
Salinity (psu)	1	NS	NS	NS	NS
Dissolved oxygen (mg/L)	1	3.92	0.0485	4.03	0.0454

resulted in substantial reductions to the CV in Gray Snapper CPUE for both size-classes; those reductions ranged from 15.5% to 71.2% (Figure 6).

DISCUSSION

Incorporating stratified-random sampling designs into fisheries surveys is widely accepted, optimizes effort, and

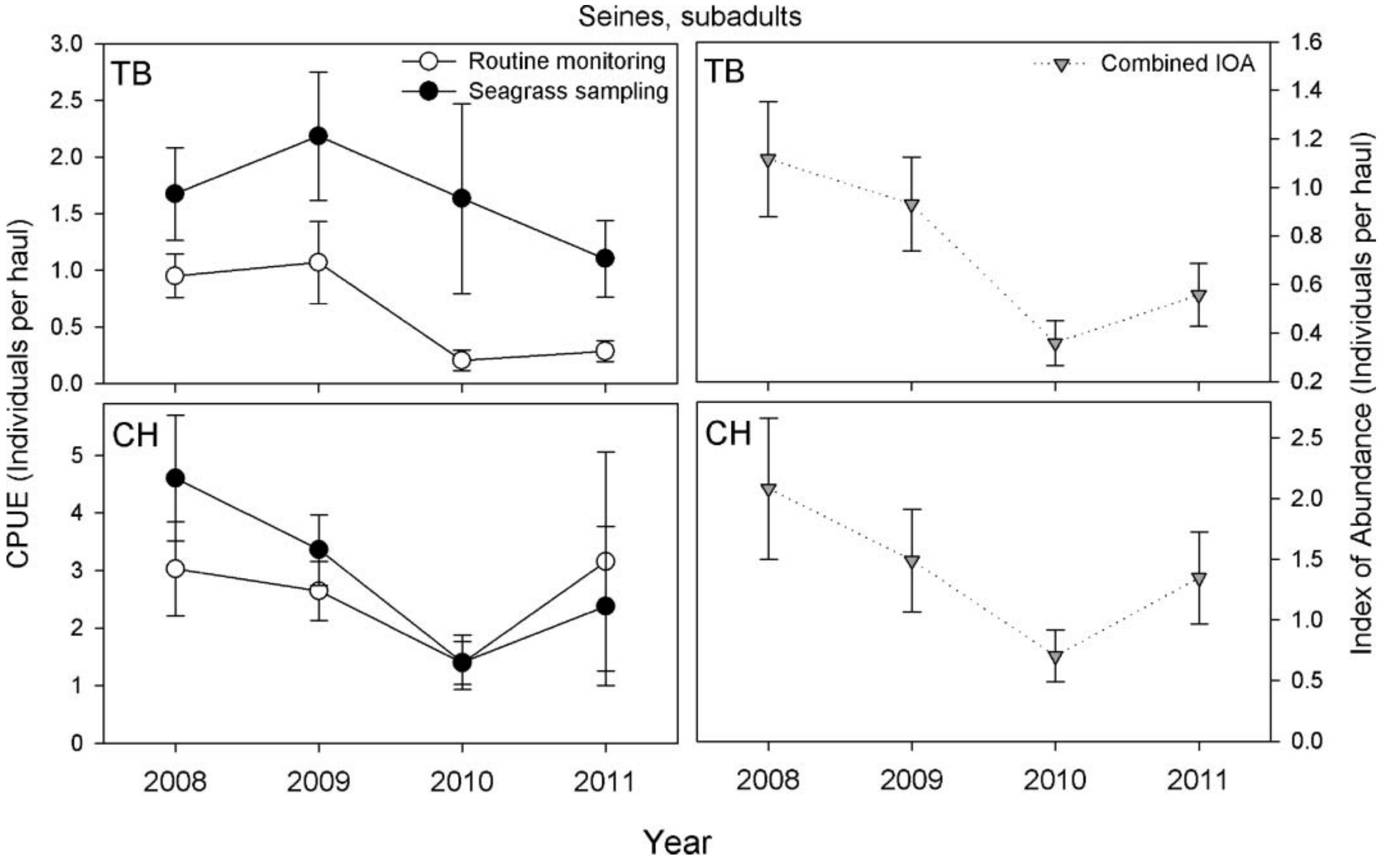

FIGURE 5. Annual CPUE (number of individuals per haul ± SE) of subadult Gray Snapper from routine monitoring (white dots) and seagrass sampling (black dots) using seines from 2008 through 2011, by estuarine system (TB: Tampa Bay; CH: Charlotte Harbor). Annual least-squares mean (number of individuals per haul ± SE) abundance (IOA) for both sampling types combined is also plotted (gray triangles). Note differences in scale on *y*-axes.

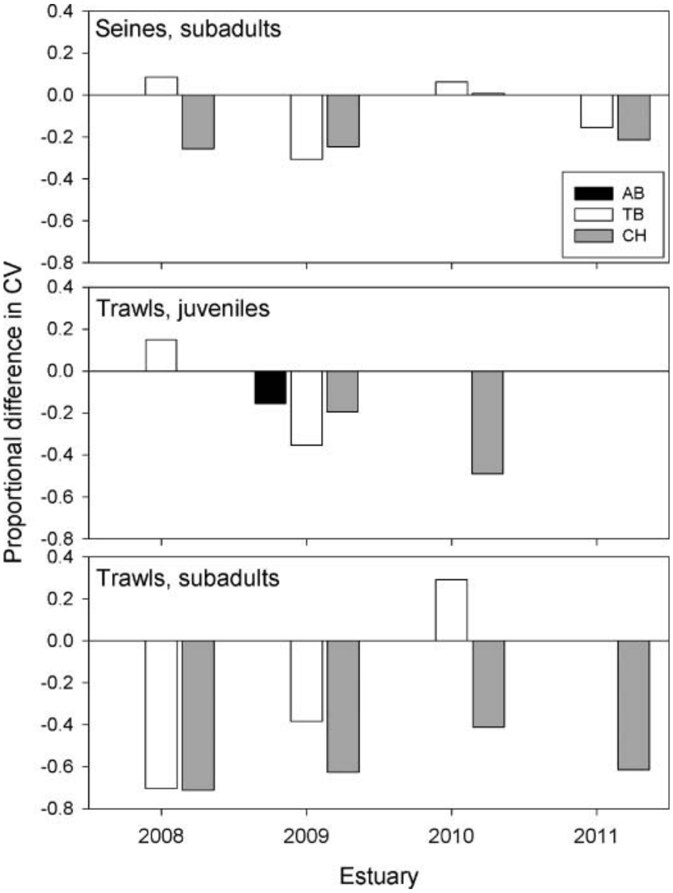

FIGURE 6. Reduction (negative numbers) in the annual coefficient of variation (CV) from routine monitoring to seagrass sampling by estuary for each gear type and size-class (AB: Apalachicola Bay, black bars; TB: Tampa Bay, white bars; CH: Charlotte Harbor, gray bars). Positive numbers indicate years in which CVs increased during seagrass sampling. Missing bars indicate that no Gray Snapper of a size-class were collected during routine monitoring. Subadults were not analyzed for Apalachicola Bay because so few were collected.

increases sampling precision and power (Kennelly et al. 1993; Ault et al. 1999; Rotherham et al. 2007; Smith et al. 2011). Careful attention to stratum designation and sample distribution can result in a design that produces more precise estimates of population abundance than would be possible with a simple random design (Gavaris and Smith 1987). Furthermore, when a species is not evenly distributed over a survey area or when a certain habitat is not sampled proportionally with a particular type of gear, a habitat-based calculation of abundance can increase precision (Rooper and Martin 2012). We have shown that targeting a stratum (polyhaline seagrass habitat) known to hold large numbers of Gray Snapper can reduce the CV and improve abundance estimates compared with routine monitoring for juveniles and subadults. Importantly, surveys of polyhaline seagrass habitats captured larger juveniles (50–100 mm SL) that were previously found to be rare (Flaherty et al. 2014), potentially providing more accurate recruitment indices since presumably this size-class has already experienced a significant portion of the natural mortality contributing to variability in recruitment (Smith 1985; Myers and Cadigan 1993a, 1993b). Trends in abundance of small juvenile Gray Snapper (≤50 mm SL) during routine monitoring in Tampa Bay and Charlotte Harbor using 21.3-m seines (Flaherty et al. 2014) reflected the same maxima and minima in abundance found in this study using trawls, adding confidence to these methods. Annual trends in subadult Gray Snapper abundance found during seine sampling were comparable over both sampling types and similar to previous trends developed using routine monitoring data (Flaherty et al. 2014), but higher catch rates during seagrass sampling improved annual indices by reducing error. Incorporating these additional samples into the indices of abundance improves the precision of these trends and provides a more complete picture of Gray Snapper abundance over time.

This study has demonstrated that seagrasses in relatively deep water (>1 m) sampled by trawls provide valuable habitat for juvenile Gray Snapper. The edges of deep, polyhaline seagrass beds often occur where light and turbidity levels approach the limits of seagrass tolerance and thus are often the first part of a bed to be harmed by the degradation of water quality (Tomasko et al. 2001; Steward et al. 2005; Crean et al. 2007). Although most historical fisheries data have been collected in shallow, easily accessible seagrass beds, these relatively deep and often very extensive seagrass beds may provide preferred habitat for some fish species in Florida. A few studies (Bell et al. 1992; Heithaus 2004; Jackson et al. 2006) have documented increasing diversity, abundance, and biomass of fish assemblages inhabiting the deep edges of seagrass beds. Our survey, which encompassed edge habitat in some sites, documented Gray Snapper habitat use of deep (>1 m) seagrass beds compared with their use of shallow shoreline habitats and deeper channel habitats. Freshwater runoff from land is more likely to influence fish inhabiting shoreline habitats, which consequently have lower salinities and greater proportions of muddy or mixed sediments than do shoal seagrass beds (DeAngelo et al. 2014). Although increased turbidity and nutrient levels along the shoreline associated with freshwater inflow may reduce predation pressure and increase the number of filter-feeding fishes or other prey (Blaber and Blaber 1980; Cyrus and Blaber 1992), the findings in this study indicate that Gray Snapper, in particular, are more often found in the seagrass beds in deeper, more saline waters targeted by our seagrass sampling efforts. The differences in average depth may seem slight between sampling types but they had a significant effect in all IOA models, may indicate microhabitat preferences, and provide better insight on habitat transitions for this species. Estuarine seagrass beds establish connectivity between emergent shoreline vegetation, such as mangroves or salt marshes, and channels and offshore reefs that are important habitats for Gray Snapper (Zieman and Zieman 1989; Yáñez-Arancibia et al. 1993; Verweij et al. 2006).

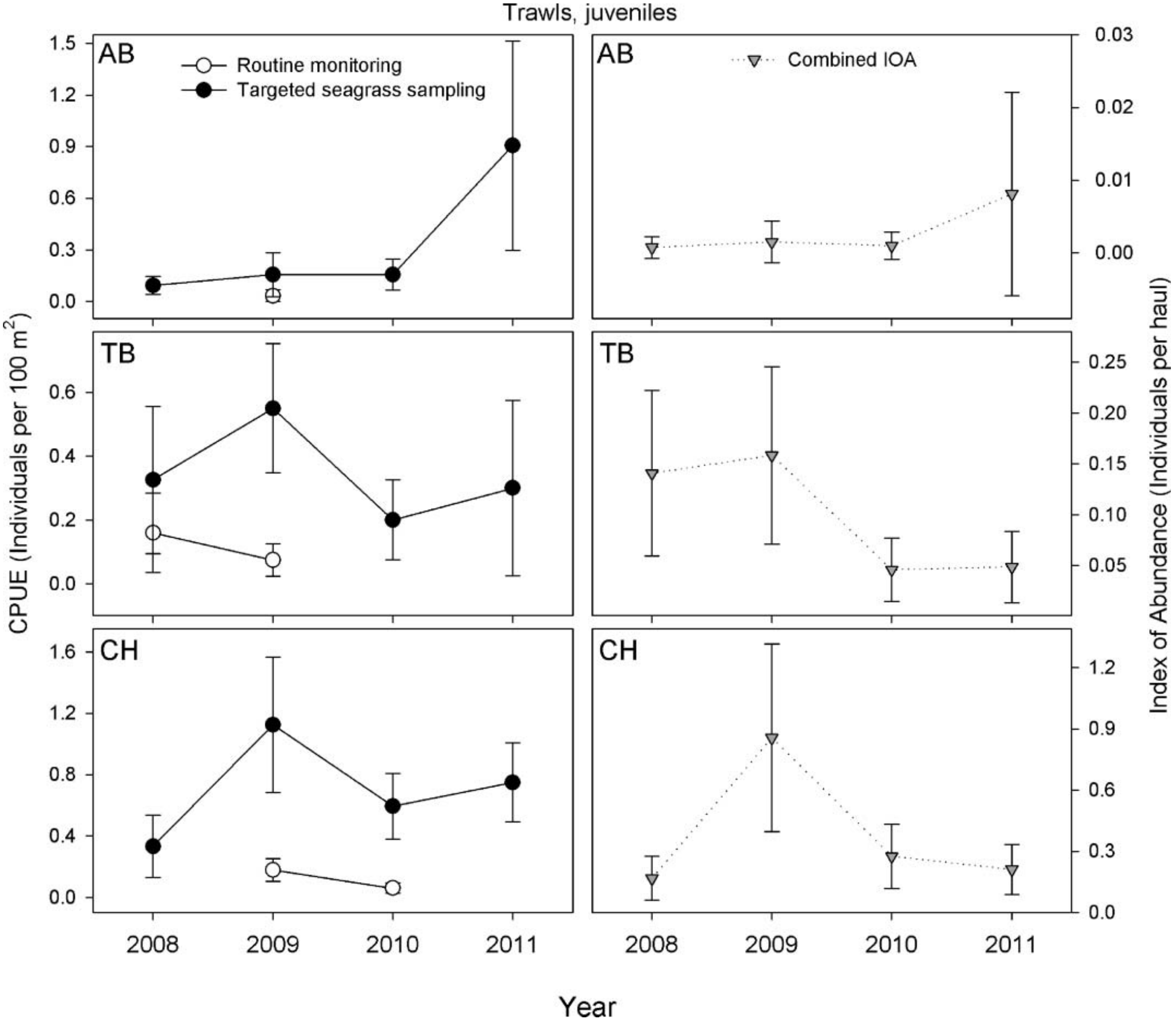

FIGURE 7. Annual CPUE (number of individuals per 100 m^2 ± SE) of juvenile Gray Snapper from routine monitoring (white dots) and seagrass sampling (black dots) using trawls from 2008 through 2011, by estuarine system (AB: Apalachicola Bay; TB: Tampa Bay; CH: Charlotte Harbor). Annual least-squares mean (number of individuals per haul ± SE) abundance (IOA) for both sampling types combined is also plotted (gray triangles). Note differences in scale on *y*-axes.

Gray Snapper probably exhibit an ontogenetic shift to deeper waters during their first year in estuarine nurseries. In previous studies, juvenile Gray Snapper were found more often in areas with a greater proportion of seagrass habitat and, in most cases, shallower water (Nagelkerken et al. 2000; Cocheret de la Morinière et al. 2002; Whaley et al. 2007; Faunce and Serafy 2008; Flaherty et al. 2014). We found that a large number of juveniles, and in particular larger juveniles (50–100 mm SL), inhabited deep seagrass areas. The tendency of these larger juvenile and subadult Gray Snapper to occupy deep seagrass habitats may indicate a migration from shallow (<1 m) seagrass and mangrove estuarine habitats to deeper seagrass and eventually structured reef habitats as they grow. An ontogenetic shift in habitat preference of Gray Snapper to deeper, polyhaline habitats is supported by the knowledge of their life history and migration patterns (Nagelkerken et al. 2000; Cocheret de la Morinière et al. 2002; Denit and Sponaugle 2004b). Some of the larger fish (>175–198 mm SL) sampled in this study may have already been sexually mature (Starck and Schroeder 1971; Manooch and Matheson 1981; Domeier et al. 1996) and preparing to move offshore. Adult Gray

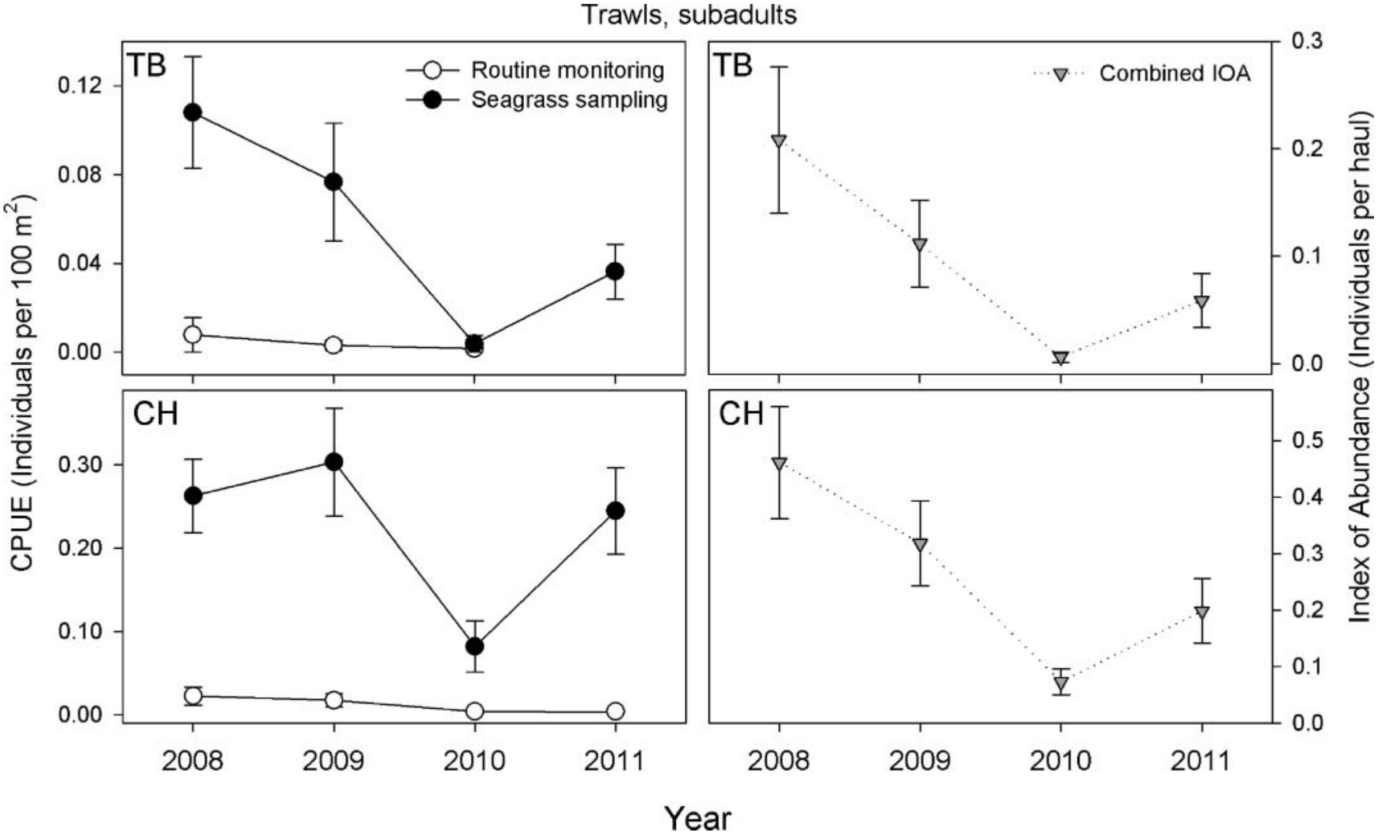

FIGURE 8. Annual CPUE (number of individuals per 100 m^2 ± SE) of subadult Gray Snapper from routine monitoring (white dots) and seagrass sampling (black dots) using trawls from 2008 through 2011, by estuarine system (AB: Apalachicola Bay; TB: Tampa Bay; CH: Charlotte Harbor). Annual least-squares mean (number of individuals per haul ± SE) abundance (IOA) for both sampling types combined is also plotted (gray triangles). Note differences in scale on *y*-axes.

Snapper staging for migrations offshore during the spawning season (May–September: Allman and Grimes 2002) have been found to use estuarine passes (Luo et al. 2009), which may partly explain the high abundance of Gray Snapper collected during our study in these deeper, polyhaline seagrass areas closer to the ocean. Larger, adult Gray Snapper have been captured using hook-and-line methods from hard-bottom areas and estuarine passes close to polyhaline seagrass beds in Tampa Bay (Switzer et al. 2011), which supports this documented movement.

TABLE 4. Results of generalized linear modeling analyses indicating the effects of year and several habitat and physicochemical variables on the CPUE (number of individuals per trawl) of juvenile Gray Snapper including data collected during seagrass sampling from May through November 2008–2011. ndf = numerator degrees of freedom, ddf = denominator degrees of freedom, NS = not significant.

		Apalachicola Bay (ddf = 246)		Tampa Bay (ddf = 231)		Charlotte Harbor (ddf = 316)	
Model variable	ndf	*F*	*P*	*F*	*P*	*F*	*P*
Year	3	2.34	0.0745	1.44	0.2323	3.82	0.0103
Sampling type	1	7.23	0.0077	NS	NS	NS	NS
Sampling type × Effort	1	NS	NS	NS	NS	NS	NS
Sampling type × Starting depth	1	5.09	0.0250	NS	NS	NS	NS
Bottom type	3	NS	NS	NS	NS	4.36	0.0136
Starting depth (m)	1	1.59	0.2082	12.17	0.0006	11.01	0.0010
Temperature (°C)	1	NS	NS	NS	NS	NS	NS
Salinity (psu)	1	NS	NS	NS	NS	NS	NS
Dissolved oxygen (mg/L)	1	NS	NS	NS	NS	NS	NS
Effort (100 m^2)	1	4.59	0.0331	NS	NS	8.92	0.0030

TABLE 5. Results of generalized linear modeling analyses indicating the effects of year and several habitat and physicochemical variables on the CPUE (individuals per trawl) of subadult Gray Snapper in two estuarine systems in the eastern Gulf of Mexico including data collected during seagrass sampling from May through November 2008–2011; ndf = numerator degrees of freedom, ddf = denominator degrees of freedom, NS = not significant.

		Tampa Bay (ddf = 410)		Charlotte Harbor (ddf = 560)	
Model variable	ndf	*F*	*P*	*F*	*P*
Year	3	7.75	<0.0001	11.54	<0.0001
Sampling type	1	NS	NS	7.89	0.0051
Sampling type × Effort	1	NS	NS	NS	NS
Sampling type × Depth	1	NS	NS	11.1	0.0009
Bottom type	3	NS	NS	NS	NS
Depth (m)	1	24.61	<0.0001	46.34	<0.0001
Temperature (°C)	1	8.48	0.0038	25.75	<0.0001
Salinity (psu)	1	NS	NS	NS	NS
Dissolved oxygen (mg/L)	1	3.99	0.0465	NS	NS
Effort (100 m^2)	1	NS	NS	NS	NS

In addition to exhibiting ontogenetic shifts by depth, Gray Snapper shift between shoreline and shoal habitat use. Flaherty et al. (2014) demonstrated that shoreline habitat containing SAV was more important to juvenile Gray Snapper than were structured shorelines (e.g., mangroves, artificial) alone. Subadult Gray Snapper, however, were less selective of shoreline habitats. Gray Snapper can use mangrove shorelines throughout their life, unlike other reef-associated species, which migrate permanently to deeper reefs when they reach a certain size-class (Nagelkerken et al. 2000; Faunce and Serafy 2007). We were able to identify the relative importance of shoreline and offshore habitat for juvenile and subadult Gray Snapper, which was problematic when only shoreline data were available (Flaherty et al. 2014). The greater abundance of Gray Snapper collected by trawls over seagrass compared with that of deep, mostly unvegetated habitat was expected, but the greater abundance of subadult Gray Snapper on shoals than on shorelines was surprising, due to their close association with mangrove habitat (Thayer et al. 1987; Ley et al. 1999; Faunce and Serafy 2008). A similar study comparing the overall nekton community associated with these two habitats also revealed that Gray Snapper did not characterize the overall shoreline fish assemblage (DeAngelo et al. 2014), so other factors such as habitat fragmentation, proximity of alternate habitats, and edge effects may be influencing Gray Snapper habitat use.

An accurate estimation and prediction of juveniles that recruit into the fished offshore adult population is critical for effective assessment and management (Smith 1993; Koenig and Coleman 1998; Coleman et al. 1999). An unpredictable relationship between juvenile and subadult Gray Snapper abundance has been observed among years and estuaries (Flaherty et al. 2014), but that may have been partly attributable to the underrepresentation of critical habitat (i.e., deep, polyhaline seagrasses and structured benthic habitats). Reductions in the CV for annual abundance were demonstrated when sampling polyhaline seagrass beds, so continued sampling of these habitats is necessary to determine whether incorporating them also improves the correlation between relative abundances of juveniles and subadults. Limitations of traditional nets in sampling structured benthic habitats (e.g., limestone rock outcrops, natural and artificial reefs) preclude sampling of additional known habitats for Gray Snapper in the estuary, so little long-term information exists on the relative importance of these habitats to reef species. Data on the occupancy of estuarine and nearshore structured habitats by larger subadults and adults (legal-size fish for harvest) should be collected to fill this gap in knowledge, further improve indices of abundance, and enhance the understanding of habitat use and ontogeny in Gray Snapper.

To conclude, we have determined that habitat-based sampling can improve estimates of Gray Snapper abundance in the estuaries examined. We also improved the utility of trawl data, which previously did not contain sufficient numbers of Gray Snapper to allow the generation of an abundance index. The affinity for seagrass habitats reported in this study complements the findings of other studies (Chester and Thayer 1990; Bartels and Ferguson 2006) and exhibits the importance of seagrass shoals and deep seagrass beds. These results highlight the advantages of examining aspects of habitat use and ecology when adapting existing monitoring programs. By evaluating available data on habitat use by species of primary interest, it is possible to develop multihabitat sampling approaches that improve abundance estimates and the understanding of species–habitat interactions without negatively affecting long-term time series provided by routine monitoring. In this case, an additional habitat was tested and successfully incorporated for future use in a long-term monitoring program. Furthermore, investigations of habitat-based sampling should be conducted for other species of interest to further aid in linking juvenile reef fish production with the offshore population and determining which estuarine habitats or regions are essential to the long-term strength of their populations.

ACKNOWLEDGMENTS

First and foremost, we acknowledge the countless personnel and volunteers of the Florida Fish and Wildlife Conservation Commission who have assisted with the collection and processing of data since the inception of this survey. Special thanks go to K. Fischer and A. Knapp for coordinating and selecting sites for the seagrass-sampling portion of this field study and to G. McLaughlin and J. P. Davis for logistical support and leadership in the field portion of the Marine Fisheries Initiative (MARFIN) grant that helped support this research. We also thank N. Cummings and R. Sadler (National Oceanic and Atmospheric Administration [NOAA], National Marine Fisheries Service [NMFS], Southeast Regional Office) for scientific insight and grant administration, respectively, during this project. Thanks to K. Fischer, P. W. Stevens, D. Chagaris, C. B. Guenther, B. Crowder, and two anonymous reviewers for providing feedback and useful editorial comments that greatly improved the quality of this manuscript, and to R. H. McMichael Jr., for his support and assistance. This project was supported in part by proceeds from sales of state of Florida saltwater recreational fishing licenses, by funding from the U.S. Department of the Interior, U.S. Fish and Wildlife Service, Federal Aid for Sportfish Restoration Project Number FL-F-F14AF00328, and from the U.S. Department of Commerce, NOAA, NMFS, MARFIN grant (NA09NMF4330152). The statements, findings, views, conclusions, and recommendations contained in this document are those of the authors and do not necessarily reflect the views of the Department of the Interior or the Department of Commerce and should not be interpreted as representing the opinions or policies of the U.S. Government. Mention of trade names or commercial products does not constitute their endorsement by the U.S. Government.

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